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Archeopsammoporus balticus gen. nov., sp. nov. (Coleoptera: Scarabaeidae: Aegialiinae), a new extinct genus and species from Baltic amber

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Abstract. A new extinct genus and species: *Archeopsammoporus balticus* gen. nov., sp. nov. is described and illustrated. The subfamily Aegialiinae Laporte, 1840 is reported for the first time from amber. A short discussion on the taxonomic position of *Archeopsammoporus* gen. nov. is given. Discussion on evolution and phylogeny of Aegialiinae is given.

INTRODUCTION

As reported by Krell (2000, 2007) Aegialiinae as fossils are known from lower Cretaceous sediments from Russia (Baysa) (Gunter et al. (2016) doubtfully cite them as middle Cretaceous sediments) and from Eocene sediments from the USA (Green River, Wyoming). Subsequently Stebnicka (2011) showed that the sediments from the USA are Oligocene and added some additional data about sediments from the Pleistocene of Canada and the USA. The description of *Psammaegialia* Nikolajev, Wang & Zhang, 2014 from lower Cretaceous sediments from China (Yixian Formation) placed by the authors in Aphodiinae, tribe Psammaegialiini Nikolajev, Wang & Zhang, 2014 in my opinion provided additional information about evolution of Aegialiinae.

Alekseev (2013) compiled a checklist of beetles from Baltic amber. Next Tamutis, Alekseev & Bukejs (2017) described first *Airapus* Stebnicka & Howden, 1996 known from amber and give some information about two other known species. Bukejs & Alekseev (2018) gave description of the next (fourth) species of Scarabaeidae known from Baltic amber. Until today only Aphodiinae among Scarabaeidae were known from Baltic amber. The present work gives description of the oldest known beetle which can clearly and unequivocally be classified to Aegialiinae. Additionally it is the only known Aegialiinae from amber anywhere.

MATERIAL AND METODS

The specimens were observed with an Nikon SMZ-U stereoscopic microscope. The photos published here were taken by the use of the Canon EOS 5D Mark III connected with Canon MP-E 65mm macro lens. Photos were edited in the Helicon Focus 7 and Adobe Photoshop Elements 2018 programs.

For morphological terms used in the description of specimens I follow mainly Stebnicka (1977).

The holotype of the new species is housed in a special, transparent, small box with printed label bearing status of the specimen, its name, name of author, and year of the designation. The holotype is part of private collection of author.

The amber with holotype was polished by hand, and was not subjected to any supplemental fixation.

The holotype is embedded a piece of amber measuring 12.7 mm x 12.2 mm.

It was not possible to make photos of specimens in all expected positions because of large light diffraction.

SYSTEMATIC PALAEONTOLOGY

Archeopsammoporus gen. nov.

Type species: Archeopsammoporus balticus sp. nov. (by monotypy)

Description. Body elongate, nearly parallel sided, total body length less than 4.0 mm.

Head transverse, only slightly convex, with a fringe of long, thick and dense macrosetae on border extended from the lower body. Clypeus gently sinuate anteriorly, distinctly, quite thinly sinuate anteriorly, simply punctate. Genae small, very widely rounded, not exceeding eyes. Frontal suture very distinct, visible as thin, transverse rib.

Pronotum slightly wider than long, with sides, anterior and hind angles widely rounded, approximately as wide as base of elytra, widest in the middle, convex, with double punctation. Sides and base bordered, anteriorly not bordered, the base is deeply grooved and hind angles are very deeply grooved. Sides with a fringe of long, thick, dense macrosetae.

Scutellum small, triangular, without punctures.

Elytra elongate, moderately convex, nearly parallel, very slightly widened posteriorly, widest near the middle; without humeral denticles; with ten striae and ten intervals. Striae distinctly, densely and coarsely punctate; punctures very distinctly indenting margins of intervals. Intervals distinctly convex, simply punctured.

Protibiae distinctly tridentate laterally, proximally with row of few, very small teeth; mesotibiae slender, with two strong transverse carinae, fimbriate apically with row of spinules of alternately unequal length. Tarsomeres very slender. Claws short, thin, weakly arcuate.

Affinity. See discussion.

Etymology. Combination of: "Archeo-" (old, long ago) and "*Psammoporus*" (the name of the most similar genus, of which it is probably an ancestor). Noun. Masculine in gender.

Archeopsammoporus balticus sp. nov. (Figs. 1-5)

Type strata. Baltic amber, mid-Eocene to Upper Eocene.

Type locality. Baltic Sea coast, Russia, Kaliningrad region, amber mine in Yantarnyi.

Type material. Holotype: adult, sex unknown, probably complete, ventral side nearly completely obscured by milky opacity.

Description. Dorsum (Fig. 1). Body length of holotype 3.6 mm, elongate, except sides of pronotum, and basal part of epipleurea glabrous, seems to be shiny.

Head (Fig. 4) trapezoidal, only slightly convex, without microreticulation. Clypeus distinctly, quite thinly bordered, very gently sinuate anteriorly, widely rounded laterally, gently notched before genae, clypeal border without macrosetae; all macrosetae visible from above are located under upper side of clypeus. Genae small, very widely rounded, not exceeding eyes, without macrosetae; all macrosetae visible from above are located under upper side of genae. Frontal suture very distinct, visible as thin, transverse rib. Clypeus simply punctate: punctures moderate to large, very dense, distance between them less than half of their diameter.

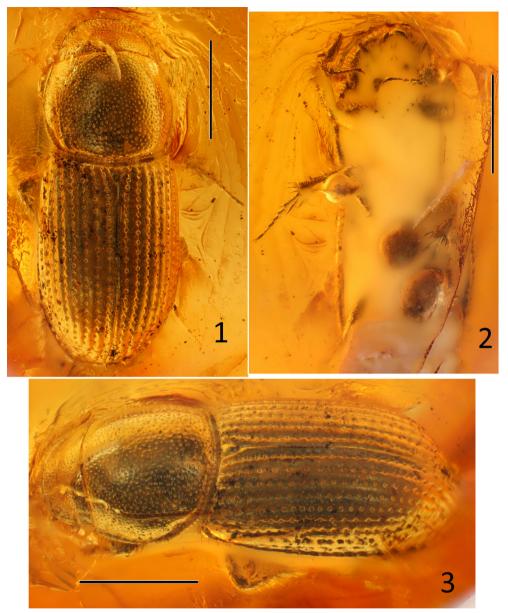
Pronotum slightly wider than long, with sides, anterior and hind angles widely rounded, approximately as wide as base of elytra, widest in the middle, convex, without microreticulation, with double punctation: larger punctures quite irregularly spaced, variable in size: moderately large to large, dense; smaller punctures irregularly spaced, very fine, quite sparse; sides and base bordered, anteriorly not bordered, wherein base is deeply grooved and hind angles are very deeply grooved; sides with long, thick, dense macrosetae, especially in anterior part.

Scutellum small, triangular, without punctures, probably with weak microreticulation.

Elytra elongate, moderately convex, nearly parallel, very slightly widened posteriorly, widest nearby the middle, probably with very weak microreticulation; without humeral denticles; with ten striae and ten intervals. Striae distinctly, densely and coarsely punctate; punctures very distinctly indenting margins of intervals. Eighth and ninth striae shortened before base. Intervals distinctly convex, distinctly, quite densely, irregularly, finely punctured.

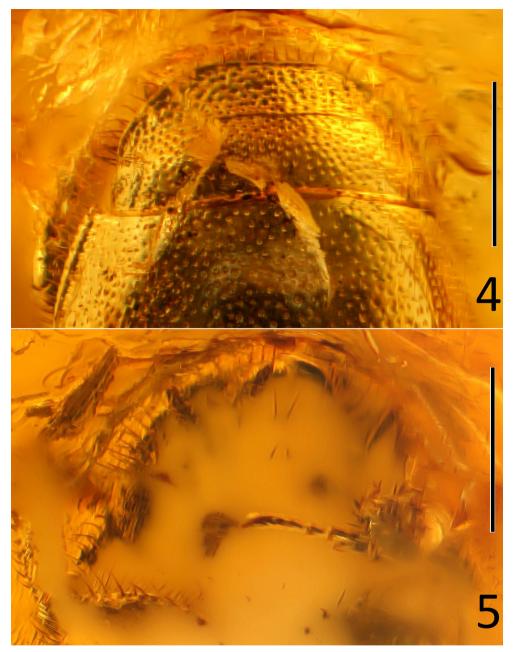
Legs very weakly visible. Profemora with dense, thick and long setae on anterior and posterior margins, with coarse, not dense punctation. Protibiae distinctly tridentate laterally, proximally with row of few, very small teeth; mesotibiae slender, with two strong transverse carinae, fimbriate apically with row of spinules of alternately unequal length. Mesotibiae with superior apical spur about twice as long as inferior apical spur and distinctly longer than basal metatarsomere, the latter distinctly longer than next two metatarsomeres combined. Claws short, thin, weakly arcuate.

Venter (Figs. 2, 5). Almost invisible, almost completely obscured by milky opacity. However, there are weakly visible mace shaped last segment of antennae, last segment of right maxillary palp and apex of very thick left mandible with distinctly visible cast in amber visible as an air-filled space; top part of apex of right mandible is also weakly visible.

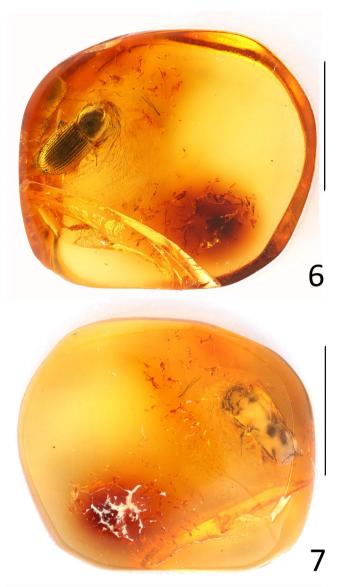


Figs. 1-3. *Archeopsammoporus balticus* sp. nov., holotype: 1- dorsal view; 2- ventral view; 3- dorso-lateral view. Figs. 1-3: scale lines: 1.0 mm.

Etymology. Toponymic; an adjective derived from the name of Baltic Sea, on the Coast of which the amber piece with the new species was collected.



Figs. 4-5. *Archeopsammoporus balticus* sp. nov., holotype: 4- head in dorso-lateral view; 5- head in ventral view; 6- dorso-lateral view. Figs. 4-5: scale lines: 1.0 mm.



Figs. 6-7. Amber piece with holotype of *Archeopsammoporus balticus* sp. nov.: 6- with specimen in dorsal view; 7- with specimen in ventral view. Figs. 6-7: scale lines: 5.0 mm.

Affinity. The newly described species belongs to an extinct taxon of Scarabaeidae. Until today, from Baltic amber, we knew only 4 species - all of them are members of Aphodiinae (exactly Eupariini), but because of distinct granules on elytra, *Saprosites succini* (Zang, 1905) is likely to belong to another genus, or even higher taxon (the holotype should be re-examined by future researchers). Additionally, 2 syntypes of *Ataenius europaeus* Quiel, 1910 were lost in World War II, and taxonomical placement of that species cannot be ascertained. Because of the shape of antennae, shape of mandibles (which are thick and massive), only

slightly convex head, characteristic genae, characteristic macrosetation visible on border on head and pronotum, protibiae distinctly tridentate, mesotibiae with strong transverse carinae, base of elytra not bordered the newly described species undoubtedly belongs to Aegialiinae Laporte, 1840. From all known extinct taxa of Scarabaeidae known from Baltic amber it can be very easily distinguished by the following combination of features: head weakly convex, with fringe of macrosetae visible on margin, with thick mandibles, sides, hind angles and base of pronotum distinctly bordered, base of elytra not bordered and intervals convex, without any tubercles.

DISCUSSION

From Pleistocene sediments, fossils of Aegialiine species are known surviving until now. The taxonomic position of Aegialia rupta Scudder, 1890 known from the Oligocene is really unknown. However, in my opinion, the taxonomic position of both species of Cretaegialia Nikolajev, 1993 is very difficult to elucidate. Cretaegialia have distinctly visible mandibles and very characteristic shape of head (wide, transverse, with clypeus rounded or truncate anteriorly, with genae not exceeding eyes, but clearly separated from rest part of clypeus) what may suggest that it is really an ancestor of present known Aegialiinae. Other features like the modified pronotum (characteristic only for Annaegialia Howden, 1971), size of body (larger than in most species of Aegialiinae known today and characteristic only of Silluvia Landin, 1949), proportions of body (similar to Aegialia Latreille, 1807) and no possibilities of precise examination of whole body make our supposition uncertain. Here it is to note that taxonomic position of Annaegialia Howden, 1971 is still debatable. Stebnicka (2009, 2011) strongly defends membership of that genus to Aegialiinae because of shape of mandibles which I agree with and because of which we cannot assign it to other subfamilies. In my opinion, because of some features so distinctly different from typical Aegialiinae (such as the shape of pronotum, shape of elytral striae and intervals) we should consider that the taxon represents a separate tribe or even subfamily. In my opinion, if we can connect *Cretaegialia* to Aegialiinae only because of its distinct, massive mandibles we should consider whether it is the ancestor of only Aegialiinae or maybe of some related subfamilies like Aphodiinae Leach, 1815 as well (at least shape of elytral striae may suggest this, but no fossils of Aphodiini Leach, 1815 older than Oligocene are known, which is troublesome). On fossils of Cretaegialia we can observe features of Aegialiinae from various genera and because of this, we can suspect that it may be an ancestor of all or almost all of the today known representatives of that subfamily.

The description of *Psammaegialia* Nikolajev, Wang & Zhang, 2014 in my opinion is much more important and helpful in phylogenetic analysis of Aegialiinae. I am not sure that both species of *Psammaegialia: abdita* and *zebrina* described in the cited work are members of the same genus or even higher taxon - I cannot assess it. In my opinion *P. zebrina* because of the proportions of pronotum, elytra, shape of pronotum, colour of elytra, shape of ventral side and rather insufficient extent of the structure preserved in the fossil question the membership of the same genus. Most useful is in my opinion the fossil of *P. abdita* - in the fossil there is distinctly visible the shape of head and pronotum. The authors, based on the understanding at

that time of the taxonomy of Scarabaeidae placed *Psammaegialia* in tribe Psammaegialiini in subfamily Aphodiinae. Additionally the name of *Psammaegialia* is in my opinion very apt. *Psammaegialia* has mandibles visible from above, which seem to be thick and massive which is a feature characteristic of Aegialiinae known today; the shape of the pronotum characteristically widened in the middle, with trace of transverse structures on it is characteristic of Psammodiini known today; however shape of head: anteriorly truncate, widely rounded on sides, very distinctly notched before genae, with genae prominent, rounded, not exceeding eyes, with trace of granules on surface of head is characteristic of both mentioned taxa (in Aegialiinae especially for genus *Aegialia*). The shape of all tibiae and its transverse ridges, apical spurs and shadows of tarsomeres (which seem to be relatively slender, approximately as long as tibiae) additionally confirm its belonging to Scarabaeidae.

The molecular study Gunter et al. (2016) showed that Scarabaeinae Latreille, 1802 evolved in middle Cretaceous and their evolution was connected with the appearance and evolution angiosperms on Earth. Most probably the evolution of Scarabaeinae was connected with the appearance of a more nutritious and less fibrous source of food.

Summarizing the above data we can suppose that *Psammaegialia* is most probably an ancestor of Aegialiinae and Psammodiini which are early evolutionary lines. Evolution of Aphodiini and probably Eupariini followed later and as in Scarabaeinae their evolution (Aphodiini certainly, Eupariini probably) was connected with the evolution and spreading of angiosperms in the middle Cretaceous. So it seems logical that Psammaegialiini should be rather treated as a higher taxon - i.e. subfamily Psammaegialiinae; and it is debatable how to treat Psammodiini, Eupariini, Aphodiini and other tribes (especially problematic with Rhypariini) in the subfamily Aphodiinae. In my opinion, finding more fossils and molecular researches should solve that problem in the future.

A member of Aegialiinae in Baltic amber at first glance seems to be unexpected. Most today's species are connected with the Holarctic region and are associated rather with a cooler climate than that of the Tertiary. However during the Tertiary climate gradually cooled down and because of that a lot of thermophilic mammals and other animals or plants became extinct at the end of this period. Recent representatives of Aegialiinae are connected with sea and lakes coasts or river banks. They usually live in roots of plants, but can also be observed walking on sand. It is to note that in the Eocene, in region where the amber piece was found, the hypothetical Eridan river formed a wide delta in which the coniferous resin from which amber was produced.

Stebnicka (1977) supposed that currently known European species of Aegialiinae are a postglacial relict of a richer Tertiary fauna. She additionally supposed that members of the genus *Psammoporus* Thomson, 1863, because of the primitive morphology of the female copulatory organs, are phylogenetically older than other Aegialiinae. The description of *Archeopsammoporus* gen. nov. partly confirms these assumptions. Aegialiinae in Tertiary most probably were much more common, widespread and numerous in species than today - otherwise finding of species which most probably lived on banks of the rivers and most probably spent a lot of time underground would be very unlikely. Additionally *Archeopsammoporus* gen. nov. seems to be a direct ancestor of the genus *Psammoporus*, but this hypothesis needs to be considered in greater detail.

Subfamily Aegialiinae Laporte, 1840 is today represented by 10 genera. The newly described genus has features of a few of them. Because of that, it most probably belonged to ancestors of genera mentioned below or to a common ancestor of these genera. It confirms the monophyletic nature of these genera. The newly described genus has an elongate body, most similar to genus Caelius Lewis, 1895. In comparison to all today known members of *Caelius* the elytra of *Archeopsammoporus* gen, nov, are very slightly widened posteriorly and general proportions of elytra are something between Caelius and Psammoporus, however, still more like in *Caelius*. Proportions of width to length of pronotum, and widely rounded sides of pronotum are nearly identical with those of the genus *Caelius*. The shape of the teeth on the protibia (directed more laterally than anteriorly) is most similar to representatives of genus Caelius. Slender tibiae and tarsomeres are much slenderer than in Psammoporus and Caelius are most close to Silluvia Landin, 1949. Tibiae with two rows of transverse carinae are characteristic for *Psammoporus* and *Silluvia*. Anterior margin of clypeus, which is very weakly sinuate and characteristically, thinly bordered is observed in most of recent representatives of *Psammoporus* and part of representatives of *Silluvia*. Hind angles of pronotum are widely rounded but with trace of modifications and because of that slightly different from that of Caelius, most similar to Silluvia, but still something between Silluvia and Psammoporus. Hind angles with widely bordered margin are most similar and characteristic to *Psammoporus*. Punctation of pronotum of which larger punctures are dense is also much more similar to *Psammoporus* and *Silluvia* than to *Caelius*. Punctation of elvtra is like in *Psammoporus*. It is to notice that very characteristic frontal suture which is very distinct and visible as a thin, transverse rib is a unique feature, not observed in any living representative of Aegialiinae, but may be observed in some of today known representatives of Aphodiini (like for example, Cnemisus Motschulsky, 1868). As a conclusion we can state: Aegialiinae as supposed by Stebnicka is old evolutionary branch and was well distinguished in Tertiary - and hence: with "older roots"; genera: Psammoporus, Silluvia and Caelius have a common ancestor and are a more closely related group among the rest of the genera in Aegialiinae - and hence recognition of the tribe Saprini Nikolajev, 2008 is unjustified, because it does not refer to a phylogenetically coherent group (or, alternatively, we should add to that group genus Psammoporus); genera Psammoporus and Aegialia not so long ago treated as one genus are evolutionary relatively far apart. In my opinion, as a supposition but backed by arguments, we should consider that Archeopsammoporus because of its most similar body plan is a direct ancestor or part of side branch of the ancestor of *Psammoporus*; *Caelius* probably has the most primitive shape of body in that group (additionally *Caelius* probably has most basal biology - for example it was collected in a flight interception trap inside a forest (Kerns, 2014)); genus Silluvia most probably is more closely related to Caelius than to Psammoporus - because of increasing variability between them.

As a final conclusion we can state that fossils, like that described above, but not only, are very useful in phylogenetic analysis and certainly help to inform our assumptions concerning the primal nature of various features and structures of body.

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